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The impact of herbicide management on long-term changes in the diversity and species composition of weed populations.

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Summary

Field vegetable systems face challenges to maintain sustainable weed management, including a reduction in available herbicides and encouragement towards reduced tillage. In a 9-year study, six herbicide products were compared, each at three rates, with a single product per plot, in a minimal cultivation system designed to exert maximum pressure for change in weed populations, to assess for predictable changes in these populations. Weed density and species number declined with increasing herbicide rate confirming that some species are able to survive reduced rates. Pre-emergence herbicides resulted in a larger number of species, greater species diversity and lower species dominance compared with post-emergence products. Species numbers increased over the first 6 years, with emergence periodicity coinciding with springtime soil disturbance. The number of species with ecological functional value increased in response to repeated use of single herbicide products. Observed species shifts illustrated a complex response to the combination of three separate drivers: changes in the dominant periodicity associated with tillage timing; a response to herbicide product and rate related to species susceptibility; and changes in community dynamics caused by variability in weather and the interaction with herbicide efficacy. Improved understanding of the effects on weed communities of the interactions between these drivers and the cropping system is essential in achieving a balance between sustainable weed management and the provision of ecological function across a range of cropping systems.

Key-words: field vegetables, tolerance, population dynamics, seedbank, sub-lethal, tillage, species shifts, functional groups, phylogenetic traits, species composition, ecology

Introduction

Weeds present both a limitation to efficient crop production and a benefit in the biodiversity they support, both directly and indirectly, in the agricultural landscape. For many decades weed scientists have focussed on the removal of weeds from cultivated fields, but we now see a paradigm shift in the attitude to weed management as a result of studies that have implicated such intensification as being significant in the decline of many farmland species, both in the UK and more widely in Europe (Stoate *et al.,* 2002). Coincident with these concerns about the role of weeds in supporting biodiversity, weed control currently faces new challenges: the loss of many products following the EU pesticide review; environmental pressure to change soil management; and a shift in our climate, which will be accompanied by as yet unquantified changes in the response of the weed flora (Davis *et al.*, 2005b). The balance has never been so delicate between maintaining the production of crops to underpin farming livelihoods, and protecting and responding to the environmental drivers that pose significant challenges to weed management.

Recent studies have shown that patterns of herbicide use in arable systems have changed significantly in the past 30 years, shifting towards a greater control of a wider spectrum of broad-leaved species (Marshall *et al*., 2001). The implications are that the species now being increasingly efficiently controlled are also species known to support invertebrate taxa important to the diet of several important bird species now in decline (Gerowitt *et al*, 2003; Marshall *et al*., 2003), leaving a set of difficult to control species with low biodiversity value. Several studies support this, reporting a significantly greater diversity of weed species both above-ground and in the seedbank in organic compared with conventional systems (Sutcliffe & Kay, 2000; Albrecht 2003).

Long-term evidence of the implications of herbicide use on the biodiversity of field vegetable crops have not been a priority, because such crops occupy only a fraction of the area of arable crops so that their ecological impact is considered significantly smaller (Grundy *et al*., 2003). In addition, there is little scope for relaxing weed management in these systems due to a low tolerance for weeds in terms of competition, quality issues, crop contamination and harvesting difficulties. Consequently, pressure remains to maintain high levels of weed management. However, the field vegetable industry has been hit hard by both the recent EU pesticide review (EU 91/414 – since the completion of this study propachlor has been made unavailable, and other herbicide products have more limited applications) and the economic disincentive, of a small size of market, for the agrochemical industry to invest in the development of new products (Gillott, 2001; Grundy *et al*., 2003). The fear is that in such minor crops a restricted range of products, combined with the current trend towards reduced application rates (frequently using a split-dose programme), may exacerbate shifts in the weed flora towards inherently tolerant species or the development of resistance (Gressel, 1995). Whether entered into voluntarily for environmental reasons or imposed through a lack of products, it is likely to be the more dominant and troublesome weed species that will benefit from reduced input systems (Barberi *et al.*, 1998; Albrecht & Sommer, 1998; Squire *et al*., 2000). Thus the reliance on a small and declining range of herbicides presents a considerable challenge to weed control in the field vegetable industry (Knott, 2002).

In addition to the challenges posed by reductions in the rate and range of herbicides, both the timing and intensity of tillage operations can have a profound influence on the composition of the weed flora. Soil management is increasingly shifting towards minimum tillage to protect vulnerable soils from erosion (Dorado & López-Fando., 2006). This may result in a change in weed flora recruitment behaviour by modifying the emergence opportunities for species with restricted germination periodicity (Froud-Williams *et al*., 1983; Chauhan *et al*., 2006) or with particular dormancy requirements and seed size characteristics (McCloskey *et al*, 1996). In arable systems there has also been a marked move towards winter, as opposed to spring cropping. This change in the time of tillage prior to crop establishment has resulted in a reduction in accumulated species richness and a shift away from the spring-germinating species known to have greater value as a food resource for other trophic levels (Hald, 1999). In contrast, field vegetable systems are inherently linked with spring cropping and are therefore biased towards a predominantly spring-germinating weed flora with a higher intrinsic biodiversity value.

A key problem in weed management is to understand and be able to predict how groups of weed species are likely to respond to all of these different challenges and drivers (Lintel Smith *et al*., 1999). This information could be used to improve the sustainability of management for crop production as well as maximising environmental benefits. The primary aim of this study was to assess changes in the above-ground weed flora in response to the challenge of a loss of herbicide products available to the field vegetable industry within the context of a shift towards minimising tillage activities.

Materials and Methods

Field trials

The field trial was made at Kirton, Lincolnshire, UK over a 9-year period (1996-2004). The site had a known flora and low presence of perennial weeds, having been used previously for field vegetable production and experimental work, receiving conventional herbicide applications during this time. The trial area was within an experimental farm, and immediately surrounded by grass headlands managed following standard farming practice. From 1996, the uncropped plots received annual applications of herbicide each spring following shallow seedbed preparation. Plots were 6 m long and two standard bed-widths (i.e. 3.66 m) wide, with a boundary of 1 m between plots. The experiment was arranged as a randomized complete block design with four blocks and 20 plots per block. Treatments comprised an untreated control (two plots per block) plus six herbicides each applied at three rates. The extra replication of the untreated (herbicide-free) control was to provide a robust base-line response against which each of the herbicide treatments could be compared, and to allow for any spatial variability in the background weed flora. Blocks were arranged to follow previous divisions of land-use and be as compact as possible, so that all plots within a block contained similar background weed flora.

To maximise the pressure for change, herbicide treatments were limited to a single application of a single product at the same rate each year. In addition, experimental plots were subjected to only a single shallow cultivation (lightly power harrowed) in the spring of each year. This was to minimise the diluting effect of the seedbank, and hence maximise the potential contribution made by the most recently shed seed from weeds that had either survived sub-lethal herbicide applications or had emerged after treatment. Each year the whole experimental area (including the control plots) was either mown or treated with a non-residual contact herbicide (glyphosate) applied to control weeds that emerged before seedbed preparation in spring, with additional spot treatments of a systemic herbicide (clopyralid) applied to kill perennial weeds (particularly thistle). All plots received these treatments simultaneously, with the choice of treatment depending on over-winter weed growth (reflecting local grower practise). The rationale for the perennial weed control was to prevent natural succession occurring and hence the crowding out and masking of more subtle responses to the experimental treatments.

The six selected herbicides were propachlor, pendimethalin and linuron (applied pre-emergence) and ioxynil, bentazone and linuron (applied post-emergence). These herbicides were among the most widely used in field vegetable crops, and representative of a range of chemical groups with different modes of action. Each herbicide was applied at either 1/4, 1/2 or full-recommended rate (Table 1), the reduced rates being included to reflect current practices and allow the assessment of the potential of reduced rates to select for resistant weed biotypes. The herbicides were applied in 400 l/ha water using an Oxford Precision Sprayer (OPS) with four nozzle (lurmark 02/F80) boom. The pre-emergence products were usually applied within 5 days of cultivation, whilst application of the post-emergence products varied according to the range of growth stages in the weeds present (Table 1 – later application reflected drier conditions). Each plot received only one annual application of a given herbicide at a given rate, with no sequential applications so that pre-emergence and post emergence treatments were separated. Although not current practise, this allowed the simple assessment of the individual effects of different herbicide products, timings and rates.

Table 1 near here

The overall treatment effects were assessed by recording the presence of weed species from two 25 cm x 25 cm quadrats, randomly placed on each plot at the start of each season and then fixed. The quadrats were positioned away from plot edges to reduce possible edge effects and varied in position each year to prevent the same patch of ground being continually assessed. Recordings were made on an approximately monthly basis through the growing season. Recordings from 1996 to 2001 were on the presence/absence of weed species. In the final three years (2002-2004) detailed records of numbers of individual plants were made for each species present in the quadrat.

Statistical analysis

The weed species presence/absence data were summarised as the total number of species and the numbers of species from four emergence period types (Supplementary Table S1) present each year on each plot (combining observations across all assessments within a year). Weed species were further classified according to various ecological traits (Supplementary Table

S1), including their importance to birds and invertebrates, and summarised in terms of overall ecological value, and occurrence and difficulty to control in typical field vegetable systems (including potatoes, spring cabbage, vining peas, dwarf beans, onions and carrots). In 2002-2004, the numbers of plants of each species were used to derive biodiversity and dominance indices (log series index α, Berger-Parker index – see Magurran (1983) for calculations) for each plot, using the late June/early July assessments in each year. These two indices were chosen because they "combine ... the advantages of being simple to calculate, easy to interpret and statistically and ecologically sound" (Magurran, 1983). Both also have a low sensitivity to sample size, a key consideration due to the potential variability in sample size caused by the sampling strategy. Analysis of variance (ANOVA) was used to detect differences caused by the timing of herbicide application (pre-emergence or post-emergence), herbicide product, and herbicide application rate, for trends across years, and for the interactions between these treatment factors. Analyses across years assumed a split-plot design, with year as a sub-plot factor and herbicide product/rate as a main-plot factor. Numbers of species present per plot were square-root transformed prior to analysis to satisfy the assumptions of homogeneity of variance.

Principal Component Analysis (PCA) (Krzanowski, 2000) was applied to the species presence/absence data from all nine years to identify shifts in the weed flora composition both over time and caused by the different herbicide application timings, products and application rates. Biplots (Krzanowski, 2000) were used to display the identified associations between treatment combinations and weed species. Separate analyses considered shifts over time (years) and due to herbicide application timing, product and application rate.

Results

Overall species numbers

The number of species changed significantly, from an initial average of five species in 1996 to a maximum average of 10.5 in 2002 (Table 2; $P<0.001$), remaining stable from 2000 onwards. Untreated control plots and those receiving reduced application rates supported more diverse floras ($P<0.001$, Fig. 1(b)). There was a peak in 2002/2003 of almost 12 species for reduced rate applications of some pre-emergence herbicides (data not shown), with a reduction for most treatments in 2003 (Fig. 1), probably caused by the dry conditions inhibiting the germination and establishment of some species in this year. Over the whole experiment, 24 different species were observed.

Figure 1 near here

Table 2 near here

Pre-emergence herbicide plots (average 9-10 species) generally supported more species than post-emergence herbicide plots (average 8-9 species) (P<0.001, Fig 1(a)). The untreated plots supported the most species, while among the herbicide treated plots, propachlor supported the most species and bentazone supported the fewest (Table 2). Linuron, applied as both pre- and post-emergence treatments, supported greater species numbers when applied pre-emergence (Fig 1(a)), indicating that the timing of application can be as important in determining the emerging flora as the choice of active ingredient. There was little evidence for any interaction between herbicide product and application rate (P=0.538), though the combined effects of herbicide product and application rate on species numbers varied across years (P=0.011, data not shown)

Biodiversity

Ecological biodiversity indices formalised the analysis of shifts in the biodiversity of the natural flora as a result of the herbicide regimes. The log series index α (indicating species richness) was higher for pre-emergence herbicides than for post-emergence herbicides (P<0.001, Table 3). The reverse was true of the Berger-Parker index (indicating dominance) for which ioxynil and bentazone treated plots (both post–emergence) had high values (P<0.001, Table 3). The greatest species richness was seen in 2002 (P<0.001, Table 3) and the greatest dominance in 2003 (largely *Poa annua* L.) (P<0.001, Table 3). Species richness increased with reduced application rate (P<0.001, Table 3) whilst species dominance decreased (P=0.095, Table 3). There was no evidence for any interaction between herbicide product and application rate for either biodiversity index (P=0.955 and 0.334 respectively, data not shown).

Table 3 near here

Changes in species profiles over time (relative presence and absence)

Groups of species with similar profiles over the course of the study were identified. For example, *Stellaria media* (L.) Vill. (species c) and *Urtica urens* L. (j) were present on almost 100% of plots in 1996 and remained common until the drought of 2002 when they were almost entirely absent, recovering towards previous levels by 2004 (Fig. 2). Similarly, *Sinapis arvensis* L. (m), *Thlaspi arvense* L. (n) and *Sonchus oleraceus* L. (u) remained present in the flora following their first appearance in 1999 (*S. arvensis*, *T. arvense*) and 2000 (*S. oleraceus*) (Fig. 2).

Fig 2 near here

Some species demonstrated more erratic behaviour. *Senecio vulgaris* L. (s), a wind-dispersed species, was initially uncommon but appeared in sizeable numbers in 1997 and 2002. This was possibly caused by chance invasions from surrounding vegetation rather than by the initial seedbank. In contrast, species such as *P. annua* (x) showed smoother long-term trends, steadily increasing in presence.

Changes in emergence strategies over time

Each of the species were classified as a) capable of emergence from spring through to the late summer and autumn (typically summer annuals), b) capable of emergence from the autumn through to the following spring (predominantly winter annuals), c) having a single pronounced period of emergence mainly in the spring and d) having a weakly defined period of emergence covering most of the year (generalists) (Supplementary Table S1). As the numbers of species increased, new species tended to be specialists with a spring-summer emergence periodicity. By 2004 generalists had declined significantly ($P<0.001$) in their proportional contribution to the flora whilst the spring-summer emerging species made a greater contribution than in 1996 (Fig. 3). However there were no effects of herbicide timing, product or rate, or differences between treated and untreated plots.

Fig 3 near here

Changes in the species composition ecological value

There was little difference in the numbers of species present, classified by importance to bird diet, between the average of the herbicide treated plots and the untreated plots, with similar contributions from species with high, intermediate and minimal ecological value. During the study there was a significant increase for all treatments in the proportion of species of intermediate ecological value to birds, relating to the increase in the number of spring-germinating species. Pendimethalin treated plots supported the greatest proportions of species of either high or intermediate ecological value to birds, with bentazone treated plots supporting the least (data not shown).

Almost two thirds of the species present during the study are of either high or intermediate ecological value to invertebrates, with a slight increase in the proportion of such species present over the first few years. However, there was little difference in the distribution of the proportions of species across the three “insect ecological value” categories between the different herbicide treatments (data not shown).

The proportion of species classified as being susceptible to herbicides (Supplementary Table S1) decreased significantly during the study for all treatments, and, conversely, the proportion of species classified as problematic in field vegetable systems increased during the study. As anticipated, most species present during the study are classified as having a large persistent seedbank. However in 2002, there was a fleeting appearance of several wind-blown species with a less persistent seedbank, such as *S. vulgaris* (s) and *Cirsium arvense* (L.) Scop (t), and of species known to be tolerant of dry conditions (*P. annua* (x)) (Fig. 2h).

Combining across these ecological traits, there is a general decline during the study in the proportion of species present that are of lower ecological value but are not problematic in field vegetable systems. There is a corresponding increase in the proportion of species with a higher ecological value but which are considered more problematic.

Long term seasonal responses dominate product differences

A first PCA (Fig. 4) assessed trends in species composition across years and due to product timing (i.e. pre-emergence, post-emergence, no product). Analysis of data for individual products and application rates across years gave similar patterns, but only combinations of product timing and year are shown here for clarity. Treatment points (e.g. 1X) close to species vectors (e.g. s) indicate an association between the treatment and weed species. Importantly, changes in species composition are more strongly associated with season than with individual herbicide treatments, with a strong trend over time but with year 7 (2002) unusual.

Fig 4 near here

Most species vectors are short (letters clustered at the origin) and are therefore not strongly associated with particular years/treatments. Proximity of a species vector to a year indicates a strong positive correlation, suggesting a transient presence or an increase in intensity for the species in that year. For example, species v (*Tripleurospermum inodorum* Schulz Bip.) and k (*Raphanus raphanistrum* L.) are strongly associated with year 7 (2002) (Fig. 4), but are present on most plots throughout the study (Fig. 2). In contrast, *U. urens* (j) and *S. media* (c) are strongly negatively correlated with year 7 (2002). Although present on most plots throughout the study (Fig. 2), these species were only found on 7 and 8 of the 80 plots respectively in 2002. Despite this limited presence in 2002, they were still present in sufficient numbers to remain amongst the dominant species on these plots. This suggests a patchy spatial behaviour and highlights how the presence-absence data could be misleading without the detailed abundance data collected from 2002 onwards. Despite spot treatments aimed at controlling perennial weeds prior to seedbed preparation, two perennial species had a notable presence during the experiment. *Rumex obtusifolius* (h) was only seen in 2002, but on about 80% of plots (Fig. 2). In contrast, *C. arvense* (t) was seen throughout the experiment, but in increasing numbers in the later years (Figs. 2 & 4).

Clear seasonal differences were observed during the last three seasons. In the absence of herbicides, *S. media* was particularly abundant in 2004 compared with 2002 and 2003 (P<0.001), but the pattern on the herbicide treated plots was complex. Both linuron and ioxynil treated plots had greatest abundance of *S. media* in 2002, suggesting an interaction between herbicide efficacy and season. Other species saw more consistent seasonal trends across treatments, such as *V. arvensis*, which significantly increased in abundance (P<0.001) and *C. arvense,* which significantly decreased in abundance (P<0.001) (Supplementary Table S2).

Product differences dominate rate effects

A second PCA assessed associations between individual products and weed species, for data combined across years (Fig. 5). A number of strong associations are indicated. For example, *T. arvense* (n) and *S. arvensis* (m) showed a strong association with propachlor (2), to which they both have resistance, as do many *Brassicaceae*. Similarly, *Fumaria officinalis* L. (a) and *P. annua* (x) are associated with linuron (1, 4) and ioxynil (5) respectively.

Fig 5 near here

There is a clear division between the application timings, with all pre-emergence products to the left, and all post-emergence products to the right (Fig. 5). The detailed abundance data (Supplementary Table S2) provides a greater insight into how the individual species responded. The most striking example was *Chenopodium album* L. (d), consistently more abundant following the pre-emergence application of linuron compared with the post-emergence application (Supplementary Table S2).

Discussion

Modifying the flora through cultivation timing and intensity

Land used for field vegetables is subjected to frequent soil disturbance events associated with seedbed preparation, sometimes with multiple sowings in a single year, and generalist, opportunistic species tend to do well in these frequently disturbed environments. Conversely, continuous cropping systems, dominated by a specific cropping regime, will tend to be dominated by weeds that mimic the life-cycle of the crop (Cardina *et al.*, 1998). The reduction in tillage frequency in this study resulted in a steady increase in the total number of species observed (Sosnoskie *et al.*, 2006), with the single springtime seedbed preparation favouring species having a major spring flush, coinciding with this disturbance, as also observed by Squire *et al*., (2000).

The lack of variation in the seasonality of the species in the untreated and herbicide treated plots suggests that cultivation timing and frequency was the major driver behind changes, rather than any herbicide effect, probably explaining the increase in *P. annua*, as grass weeds have been frequently reported as being associated with reduced tillage regimes (Davis *et al*., 2005a). Perennial species did not initially feature in significant numbers within the seedbank, probably because of the frequent soil disturbance associated with the land management prior to the start of the experiment. The establishment of such species under the reduced disturbance tillage regime (Froud-Williams *et al*., 1983; Tuesca *et al*., 2001) resulted in their appearance after about three years.

Herbicides as management tools for determining species dominance

As the experimental site had been subjected to many years of conventional intensive weed control, with multiple, diverse herbicide applications, it was not surprising that the single annual application of a single product provided opportunities for species numbers to increase. While several studies have reported that reduced weed management leads to an increase in species diversity (Albrecht, 2003), it can also amplify the presence of dominant and difficult to control species (Squire *et al*., 2000). The increasing dominance of some species (e.g. *P. annua* on the bentazone and ioxynil treated plots) could be reasonably explained by the resistance of species to products, but results for other species were less easily explained based on known herbicide susceptibility. *Veronica persica* Poiret had become the most frequent species by 2004, yet is known to be susceptible to all the products (moderately susceptible to bentazone) used in the study. So susceptibility to an active ingredient could not be used in isolation to explain the observed dominance, maybe reflecting an adaptation in emergence timing for this generalist species.

Propachlor treated plots had significantly greater species richness ($P<0.001$) and lower species dominance compared with the untreated control, suggesting that the selective nature of this product was removing dominant species from the flora and creating a gap for other species. More generally, the earlier application times of the pre-emergence products (3-7 weeks earlier than the post-emergence application times) allowed the exploitation of this period by species that germinated after herbicide efficacy had declined. Hence the application and timing of a specific herbicide can enhance the presence of a species by removing competitors (Supplementary Table S2), supporting the hypothesis that herbicides have the potential to modify the weed flora composition as a selective management tool (Pywell *et al*., 1998).

Reduced herbicide application rates provide opportunities for species to escape control

The untreated plots, and those receiving the lower rates of all products, supported a more diverse flora than the full rate plots. The more diverse flora resulted from reduced rates being sub-lethal to seedlings from a wider range of species than when herbicides were applied at the full recommended rate. Herbicide efficacy may also be more sensitive to the growth stages of the weeds when applied at reduced rates (Sønderskov *et al.*, 2006). For pre-emergence herbicides, reduced rates may remain effective for only a short time so that late-emerging seedlings may survive. These factors all lead to opportunities for a greater range of species to contribute to the flora. Squire *et al.* (2000) reported such increases in abundance for less intensive regimes using reduced herbicide rates, with a stabilization of the number of species occurring between the third and sixth years, broadly reflecting our study. Bostrom & Fogelfors (2001) demonstrated that reduced herbicide application rates increased the proportion of "difficult-to-control weeds", as observed in this study. However population variation means that early detection of small changes in response to herbicides is likely to be difficult (Collings *et al.*, 2001). Sub-lethal herbicide applications may also contribute to changes in the flora through subtle effects on the germination, competitive ability or fecundity of the progeny of treated maternal plants (Champion *et al.,* 1998; Grundy *et al.,* 1995; Hald, 1999). The relative importance of these maternal effects is largely unknown and further information is required to assess the implications of reduced herbicide application rates on subsequent weed population shifts. The relationships between application timing, herbicide rate and weed species/herbicide interactions are therefore likely to be complex (Andersson, 1996).

Can the responses of species to specific herbicides be predicted?

Active ingredients in herbicides are species specific, but weed species belonging to the same family or order may respond similarly to a particular product. In this study several species showed strong associations with the product to which they are known to show resistance, appearing with higher frequency on plots treated with that product (Supplementary Table S1 & Fig. 4). Other studies have shown similarities between species from the same family in their susceptibility to particular herbicides (Bond, 1988). However, there are clearly anomalies within families and the relationships are complex, with species that belong to the same order sometimes behaving very differently. The potential predictive capacity of the phylogenetic associations between weed species has not yet been seriously pursued. Screening studies of representative species from several clades against a wide range of herbicides would be required to assess the potential of a phylogenetic approach to predict the responses of species not included on product labels.

Seasonal differences dominate annual variation in the weed flora

The observed weed flora represents the effects of a complex interaction of season, application rate, product and cropping system. The selective nature of the products and the pre- or post-emergence application timing were thought to be the primary drivers of change in the weed flora. However there also appeared to be strong seasonal impacts on herbicide effects (P<0.001) (Tables 2 & 3; Supplementary Table S2).

Local meteorological records (data not shown) indicated that the period from autumn 2001 to autumn 2002 (the 2002 growing season) was the driest of the 9 years studied (April and June were particularly dry), and that temperatures for the period January 2002 to June 2002 were warmer than the 9-year average. The previous season (February 2001 to September 2001) had been wetter than comparable seasons on average. This combination of conditions led to the reduced survival of species more suited to cooler or more humid conditions, or sensitive to drought (e.g. *S. media* and *U. urens*) (Bond *et al*., 2006), creating opportunities for species that can germinate in drier conditions (e.g. *C. album*) (Qasem, 1993). Additionally, these warm spring conditions may not have provided sufficient winter chilling to break seed dormancy in species such as *Polygonum aviculare* L. (Batlla & Benech-Arnold, 2003), which were under-represented in 2002 (Fig. 2). Thus understanding the ecological responses of weed species to meteorological factors can provide a valuable but coarse insight into the changes in floral composition in a given year, without the need for complex mathematical modelling.

The interaction between meteorological conditions and herbicide efficacy is another important consideration (Riethmuller-Haage, 2006). As well as tolerating the dry conditions of 2002, *C. album* was noticeably abundant on the plots treated with bentazone, reflecting the reduced efficacy of this product against this species in dry conditions (Taylor *et al*., 1980). Gaps in the control of species, created by interactions between herbicide choice and meteorological conditions, can lead to simple niche exploitation by other species present in the seedbank. This is illustrated by the complementary occurrence patterns of *C. album* and *P. annua*, which tends to do less well in dry conditions (Mitich, 1998). Species dominance is shifted in the wetter years of 2003 and 2004, where presumably the control efficacy of *C. album* by bentazone was improved and the bentazone-resistant species, *P. annua*, was able to re-occupy the niche (Supplementary Table S2).

Broad patterns of response to management in terms of the ecological value of the flora

An emerging feature, emphasising the importance of improving our ecological understanding of weed management, is that certain cropping systems no longer require the removal of all weeds. Some common weed species contribute to supporting biodiversity in the agri-environment (Marshall *et al*., 2003) with the approach also benefiting the management of rarer species (Gibson *et al.*, 2006). This study clearly supports the generally held principles that a relaxation of weed control and a shift towards spring cultivation events will lead to a proliferation of a diverse and ecologically beneficial weed flora. While current market forces and quality expectations in field vegetable systems limit such relaxation, the approaches used in this study demonstrate the applicability of these principles to other cropping systems with seedbanks containing spring-germinating, broad-leaved weeds. Paradoxically, species providing the most beneficial ecological functions are often those most common and problematic to control within field vegetable systems. Thus a good understanding of the community dynamics of weed populations is required for the identification of management regimes, such as sacrificial areas (Grundy *et al.*, 2003), that are sustainable, economically feasible and deliver beneficial ecological functions.

To enable the assessment of the impacts of specific components of a weed management strategy, this study used a simplified version of the field vegetable cropping system into which the developed principles might be applied. In practise, weed communities will be influenced by a range of other factors (Andreasen & Skovgaard, 2009), including crop rotation, crop type, and soil type and structure, with the presence of any crop increasing the competition for resources compared with our experimental system. It is also unlikely that the same herbicide would be repeatedly and solely applied to the same field over a number of years, primarily because of variability in the crops being grown within a particular rotation, so that, in practise, the sequence of herbicides used over a number of years would prevent a strong propagation of weeds adapted to the management strategy for a particular crop. This study therefore provides an insight into specific elements of a weed management strategy, but the results require considerable integration with these other factors to provide a clear understanding of these complex systems.

Making sense of complexity: from data to models

Despite the identification of patterns associated with the main drivers (herbicide susceptibility, application rate, application timing and tillage timing) of change, there are a number of inconsistencies when examining the data on a season by season basis, such that any one of these drivers cannot be used in isolation to explain the observations. This is a result of the multiple and complex interactions between the factors involved, including the weather (Swanton *et al*., 2006). These interactions help to explain observed patterns, such as the proposed explanation for the shift in dominance between *P. annua* and *C. album* on the bentazone treated plots, but predicting future trends is more difficult. A much broader study, involving both a wider range of meteorological conditions (both different field sites and different starting years), a greater diversity of initial weed flora compositions (different field sites), and different cropping factors would be needed to develop predictive models. Even then, extreme scenarios may not be observed, limiting the capacity of such models to predict the causes of these events.

Interactions between the major management factors and ecological responses to biotic factors, such as the degree of winter chilling available for dormancy breaking, or drought tolerance during the critical establishment phase, are responsible for much of the seasonal variability. As these interactions are difficult to observe, a modelling approach is needed to understand the complexity of the system and predict responses with sufficient detail to be of practical value across a range of scenarios. Several researchers have questioned the practicality of constructing predictive models to describe weed community changes. Freckleton and Stephens (2009) proposed that short-term detailed responses of absolute numbers at a local scale may be difficult to predict with accuracy, largely because of the seasonal variation we highlight in this study. However, they state that predictions of long-term shifts in response to broad-scale patterns of management may be possible, helping to devise sustainable management strategies. We suggest that while management approaches will predominantly affect the species traits needed for success under a particular regime, it is the biotic factors that will determine which species with these traits will dominate within a particular season.

Conclusions

This long-term study has provided unique insights into how the weed flora responds over time to different management and environmental pressures, which have much wider consequences. This is largely because field vegetable systems, by their very nature, often occupy lighter, freely draining, soils known to support a higher floral diversity. This, combined with predominantly spring cropping, results in a prevalence of species known for their high ecological value in the agricultural landscape. Thus whilst a "zero tolerance" for weeds may remain a primary aim for the field vegetable industry, the ecological responses observed in the weed flora in this study may be valuable on a wider generic level. In this wider ecological context we have identified the management drivers that both pose the greatest threats in terms of their negative impacts and promotion of "difficulty to control" weed species in field vegetable systems, and support the greatest functional biodiversity in terms of services to bird and invertebrate communities. This study illustrates the potential to use a selective programme of herbicides and tillage to manage weeds within a cropping system, and to manipulate the long-term weed flora composition and dominance over time. There were three main conclusions from the study. Firstly, that pre-emergence products and reduced application rates consistently encouraged a greater species diversity compared with post-emergence products. Secondly, that there was a seasonal increase in spring emerging species, coinciding with the timing of the main tillage operation. And finally, that there was an increase in the number of species with a greater ecological functional value in response to the repeated use of a single product, spring tillage reduced input regime. Further interpretation of these data is needed, and the idea of management filters (Smith, 2006; Storkey, 2006) could provide a pragmatic approach to understanding weed community dynamics and identifying sustainable weed management strategies based on this study.

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Figure legends

Fig. 1 Changes in the mean numbers of species per plot over time: (a) comparisons of the untreated control with each of the herbicide products (responses averaged across application rates); (b) comparisons of the untreated control with each of the application rates (responses averaged across herbicide products). Back-transformed means obtained from ANOVA of square-root transformed data (Table 2). Untreated control = × (solid line), pre-emergence linuron = ○ (solid line), pre-emergence propachlor = ○ (dotted line), pre-emergence pendimethalin = ○ (dashed line), post-emergence linuron = ● (solid line), post-emergence ioxynil = ● (dotted line), post-emergence bentazone = ● (dashed line), full recommended rate = ▲ (solid line), half rate = ▲ (dotted line), quarter rate = ▲ (dashed line).

Fig. 2 Frequency of occurrence of 24 weed species across the 80 experimental plots: (a) mean percentage occurrence across all nine seasons; (b) – (j) difference in percentage occurrence for each year (1996 – 2004 respectively) compared with the mean percentage occurrence across all nine seasons. A zero value indicates no difference from the mean, a positive value indicates a greater occurrence of the species than the mean, and a negative value indicates a lesser occurrence. Species codes are: a – *Fumaria officinalis*; b – *Papaver rhoeas*; c – *Stellaria media*; d – *Chenopodium album*; e – *Bilderdykia convolvulus*; f – *Polygonum lapathifolium*; g – *Polygonum aviculare*; h – *Rumex obtusifolius*; i – *Viola arvensis*; j – *Urtica urens*; k – *Raphanus raphanistrum*; l – *Capsella bursa-pastoris*; m – *Sinapsis arvensis*; n – *Thlaspi arvense*; o – *Sisymbrium officianale*; p – *Lamium purpureum*; q – *Veronica persica*; r – *Aethusa cynapium*; s – *Senecio vulgaris*; t – *Cirsium arvense*; u – *Sonchus oleraceus*; v – *Tripleurospermum inodorum*; w – *Elytrigia repens*; x – *Poa annu.* An asterisk against a species code indicates that the species did not appear on any plots in that year.

Fig. 3 Relative contributions to the weed flora of species with different emergence periodicities, as defined in Supplementary Table S1, for a) untreated and b) herbicide treated plots in the nine years of the study, where ■ = autumn-spring; □ = spring only; ■ = spring-autumn; ■ = generalist.

Fig. 4 Biplot displaying the associations between weed species and combinations of year and herbicide application timing, as given by the first two dimensions from a Principal Component Analysis of the weed species presence/absence data averaged across replicates, herbicide products and application rates. Lower-case letters and associated vectors from the origin indicate the weed species loadings (codes as given in Figure 2 – key species are: c – *S. media*, d – *C. album*, f – *P. lapathifolium*, g – *P. aviculare*, h – *R. obtusifolius*, j – *U. urens*, k – *R. raphanistrum*, m – *S. arvensis*, n – *T. arvense*, s – *S. vulgaris*, t – *C. arvense*, u – *S. oleraceus*, v – *T. inodorum*). Numbers and upper-case letters indicate the scores for combinations of year (1 = 1996, 2 = 1997, 3 = 1998, 4 = 1999, 5 = 2000, 6 = 2001, 7 = 2002, 8 = 2003, 9 = 2004) and herbicide application timing (X = pre-emergence, Y = post-emergence, Z = untreated control). Arrow indicates the general trend from the first year to the last year of the study.

Fig. 5 Biplot displaying the associations between weed species and combinations of herbicide product and application rate, as given by the first two dimensions from a Principal Component Analysis of the weed species presence/absence data averaged across years. Lower-case letters and associated vectors form the origin indicate the weed species loadings (codes as given in Figure 2 – key species are: a – *F. officinalis*, f – *P. lapathifolium*, g – *P.*

aviculare, l – *C. bursa-pastoris*, m – *S. arvensis*, n – *T. arvense*, p – *L. purpureum*, q – *V. persica*, s – *S. vulgaris*, t – *C. arvense*, u – *S. oleraceus*, x – *P. annua*). Numbers and upper-case letters indicate the scores for combinations of herbicide product (1 = pre-emergence linuron, 2 = pre-emergence propachlor, 3 = pre-emergence pendimethalin, 4 = post-emergence linuron, 5 = post-emergence ioxynil, 6 = post-emergence bentazone) and herbicide application rate (F = full recommended rate, H = half rate, Q = quarter rate).

Table 1 Details of herbicide products, application rates and application dates for each year from 1996 to 2004. All pre-emergence products were applied on the same date in any given year, similarly all post-emergence products were applied on the same date in a given year. Pre-emergence products generally applied 5 days after cultivation, whilst post-emergence products applied according to the manufacturers recommended weed growth stage (generally the 2 true leaf stage).

Herbicide product	Rate of active ingredient applied (l/ha in 400 l/ha)			Experimental season								
	Full	Half	Quart	1996	1997	1998	1999	2000	2001	2002	2003	2004
Pre-emergence products												
Linuron (as Linuron Fl (Ashlade), 480 g/l/)	1.70	0.85	0.43	27/4/1996	1/5/1997	13/5/1998	30/4/1999	9/5/2000	30/5/2001	17/5/2002	15/5/2003	26/5/2004
Propachlor (as Ramrod Flo, 480 g/l)	9.00	4.50	2.25	27/4/1996	1/5/1997	13/5/1998	30/4/1999	9/5/2000	30/5/2001	17/5/2002	15/5/2003	26/5/2004
Pendimethalin (as Sovereign 400, 400 g/l)	3.30	1.65	0.83	27/4/1996	1/5/1997	13/5/1998	30/4/1999	9/5/2000	30/5/2001	17/5/2002	15/5/2003	26/5/2004
Post-emergence products												
Linuron (as Linuron Fl (Aslade), 480 g/l)	1.70	0.85	0.43	6/6/1996	23/5/1997	17/6/1998	10/6/1999	30/6/2000	2/7/2001	29/6/2002	29/5/2003	16/6/2004
Ioxynil (as Totril, 225 g/l)	2.80	1.40	0.70	1/5/1997	23/5/1997	17/6/1998	10/6/1999	30/6/2000	2/7/2001	29/6/2002	29/5/2003	16/6/2004
Bentazone (as Basagran 480 g/l)	3.00	1.50	0.75	1/5/1997	23/5/1997	17/6/1998	10/6/1999	30/6/2000	2/7/2001	29/6/2002	29/5/2003	16/6/2004

Table 2 Mean numbers of species per plot for each year overall, and for each herbicide product and application rate in each year. Square root transformed means shown in parentheses alongside back-transformed means. All SEDs are based on 488 d.f.

Treatment	1996		1997		1998		1999		2000	
Overall	4.84	(2.28)	9.24	(3.10)	8.56	(2.99)	8.37	(2.96)	10.43	(3.29)
Untreated Control	5.81	(2.49)	10.11	(3.24)	8.72	(3.02)	9.22	(3.10)	11.97	(3.51)
Herbicide:										
Pre-emergence										
Linuron	5.22	(2.37)	8.19	(2.93)	7.98	(2.89)	9.11	(3.08)	9.79	(3.19)
Propachlor	4.43	(2.19)	9.72	(3.18)	8.39	(2.96)	8.51	(2.98)	11.26	(3.41)
Pendimethalin	5.50	(2.42)	9.02	(3.07)	8.59	(3.00)	9.12	(3.08)	11.64	(3.47)
Post-emergence										
Linuron	4.97	(2.31)	9.20	(3.10)	8.72	(3.02)	7.88	(2.87)	9.41	(3.13)
Ioxynil	3.69	(2.02)	9.63	(3.16)	9.20	(3.09)	7.03	(2.72)	10.36	(3.28)
Bentazone	4.70	(2.25)	9.15	(3.09)	8.39	(2.96)	8.12	(2.92)	9.26	(3.10)
Application Rate										
Full Rate	3.90	(2.07)	8.69	(3.01)	8.46	(2.97)	7.93	(2.88)	9.70	(3.17)
Half Rate	5.01	(2.32)	9.51	(3.14)	8.55	(2.99)	8.08	(2.91)	10.32	(3.27)
Quarter Rate	5.35	(2.39)	9.25	(3.10)	8.61	(3.00)	8.84	(3.04)	10.79	(3.34)

Treatment	2001		2002		2003		2004	
Overall	10.50	(3.30)	10.47	(3.29)	9.49	(3.14)	9.41	(3.13)
Untreated Control	10.86	(3.35)	10.60	(3.31)	11.24	(3.41)	10.34	(3.27)
Herbicide:								
Pre-emergence								
Linuron	10.96	(3.37)	10.95	(3.37)	9.16	(3.09)	9.81	(3.19)
Propachlor	10.20	(3.25)	11.36	(3.43)	11.81	(3.49)	10.54	(3.30)
Pendimethalin	10.54	(3.30)	10.52	(3.30)	10.66	(3.32)	9.60	(3.16)
Post-emergence								
Linuron	11.14	(3.39)	9.56	(3.15)	8.04	(2.90)	7.25	(2.76)
Ioxynil	11.06	(3.38)	10.79	(3.34)	8.50	(2.98)	10.06	(3.23)
Bentazone	8.97	(3.06)	9.62	(3.16)	7.97	(2.89)	8.81	(3.03)
Application Rate								
Full Rate	10.39	(3.28)	10.00	(3.22)	8.68	(3.01)	8.66	(3.01)
Half Rate	10.07	(3.23)	10.63	(3.32)	9.51	(3.14)	9.51	(3.14)
Quarter Rate	10.95	(3.37)	10.73	(3.33)	9.75	(3.18)	9.78	(3.19)

SEDs

For comparing overall means between Years = 0.036
For comparing means for the Untreated Control between Years = 0.113
For comparing means for each Herbicide between Years = 0.092
For comparing means for each Application Rate between Years = 0.065

For comparing means for two Herbicides within a Year = 0.094
For comparing means for the Untreated Control and a Herbicide within a Year = 0.105
For comparing means for two Application Rates within a Year = 0.067
For comparing means for the Untreated Control and an Application Rate within a Year = 0.094

Table 3 Mean diversity (Log series index α) and dominance (Berger-Parker) indices for each year overall, for each herbicide product, for each herbicide application rate and for each product and rate in each year. Indices calculated from the late June or early July assessments in 2002, 2003 and 2004 only.

	Log series index α				Berger-Parker index			
Year	2002	2003	2004	Overall	2002	2003	2004	Overall
Treatment								
Overall	2.71	1.90	1.80	2.14	0.439	0.590	0.508	0.513
Untreated Control	2.83	2.06	2.15	2.35	0.398	0.409	0.382	0.396
Pre-emergence Herbicides								
Linuron	2.64	1.82	1.67	2.04	0.405	0.529	0.530	0.488
Propachlor	2.98	3.19	2.11	2.76	0.384	0.377	0.383	0.381
Pendimethalin	2.61	1.84	2.00	2.15	0.434	0.508	0.506	0.483
Post-emergence Herbicides								
Linuron	2.92	1.49	1.25	1.88	0.368	0.606	0.675	0.549
Ioxynil	2.90	1.49	1.96	2.12	0.436	0.860	0.539	0.612
Bentazone	2.15	1.46	1.58	1.73	0.638	0.785	0.497	0.640
Application Rate								
Full Rate	2.67	1.78	1.57	2.01	0.467	0.689	0.587	0.581
Half Rate	2.59	2.04	1.77	2.13	0.459	0.601	0.500	0.520
Quarter Rate	2.84	1.83	1.94	2.20	0.407	0.542	0.477	0.475

SEDs for analysis of:	Log series index α	Berger-Parker index
For comparing overall means (58 d.f.)		
for two Herbicides	0.127	0.0332
for the Untreated Control and a Herbicide	0.142	0.0371
for two Application Rates	0.090	0.0235
for the Untreated Control and an Application Rate	0.127	0.0332
For comparing means between Years (121 d.f.)		
overall	0.078	0.0165
for the Untreated Control	0.245	0.0520
for each Herbicide	0.200	0.0425
for each Application Rate	0.142	0.0300
For comparing means within a Year (121 d.f.)		
for two Herbicides	0.207	0.0480
for the Untreated Control and a Herbicide	0.231	0.0537
for two Application Rates	0.146	0.0340
for the Untreated Control and an Application Rate	0.207	0.0480

Fig 1 (a)

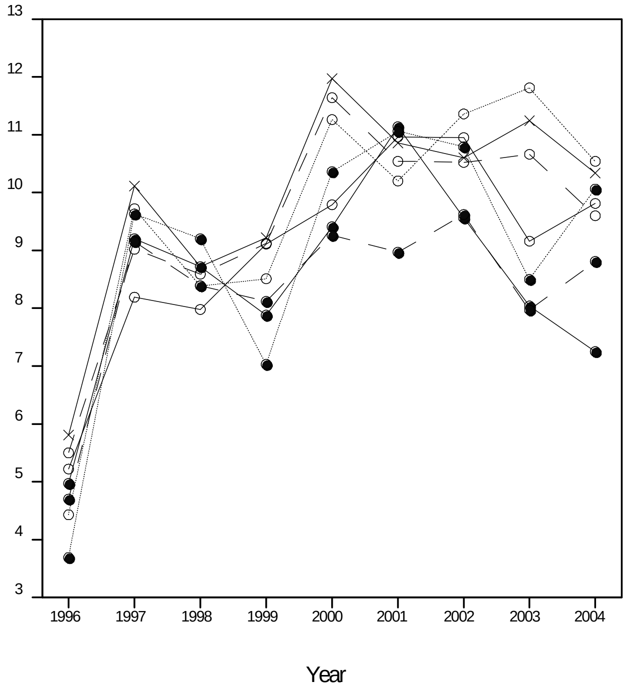

Fig 1 (b)

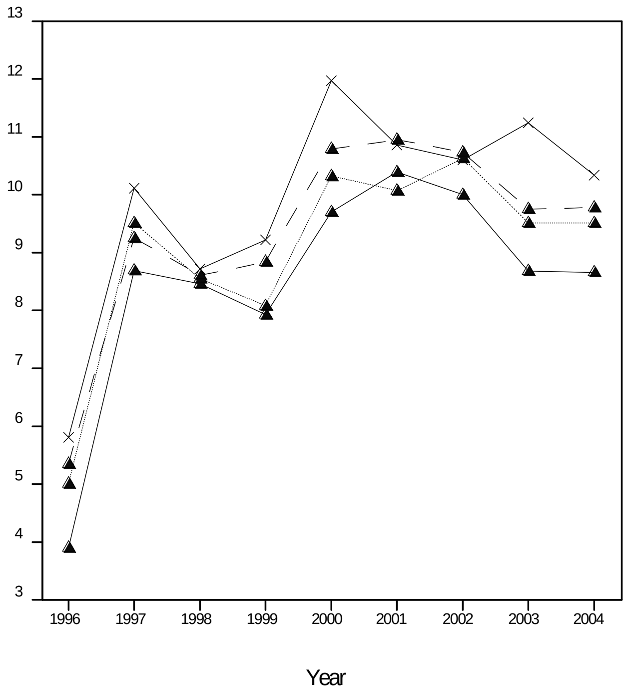

Fig. 1 Changes in the mean numbers of species per plot over time: (a) comparisons of the untreated control with each of the herbicide products (responses averaged across application rates); (b) comparisons of the untreated control with each of the application rates (responses averaged across herbicide products). Back-transformed means obtained from ANOVA of square-root transformed data (Table 2). Untreated control = × (solid line), pre-emergence linuron = ○ (solid line), pre-emergence propachlor = ○ (dotted line), pre-emergence pendimethalin = ○ (dashed line), post-emergence linuron = ● (solid line), post-emergence ioxynil = ● (dotted line), post-emergence bentazone = ● (dashed line), full recommended rate = ▲ (solid line), half rate = ▲ (dotted line), quarter rate = ▲ (dashed line).

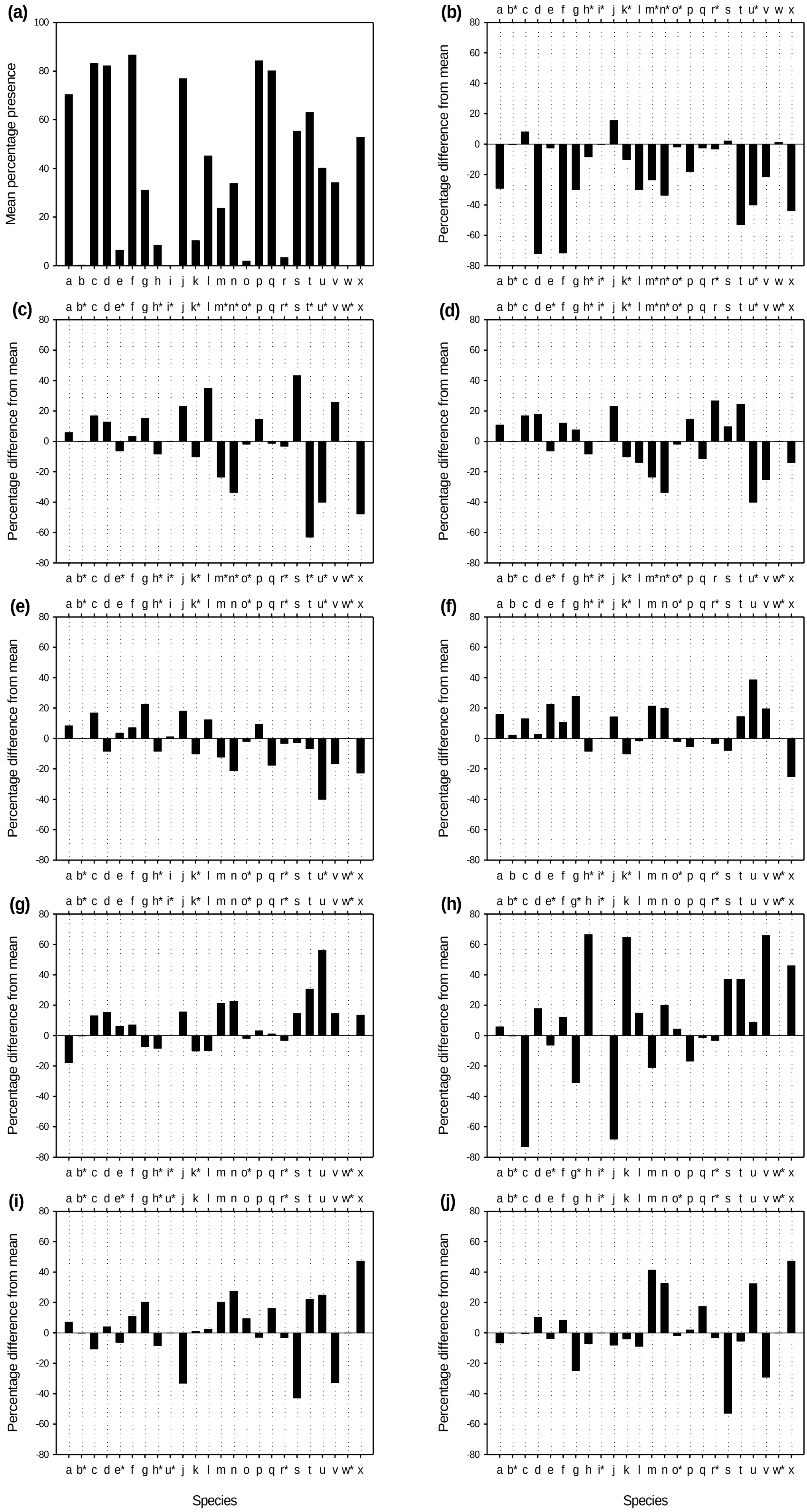
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
Mean percentage presence
Percentage difference from mean
a b c d e f g h i j k l m n o p q r s t u v w x
Species
Species

Fig. 2 Frequency of occurrence of 24 weed species across the 80 experimental plots: (a) mean percentage occurrence across all nine seasons; (b) – (j) difference in percentage occurrence for each year (1996 – 2004 respectively) compared with the mean percentage occurrence across all nine seasons. A zero value indicates no difference from the mean, a positive value indicates a greater occurrence of the species than the mean, and a negative value indicates a lesser occurrence. Species codes are: a – *Fumaria officinalis*; b – *Papaver rhoeas*; c – *Stellaria media*; d – *Chenopodium album*; e – *Bilderdykia convolvulus*; f – *Polygonum lapathifolium*; g – *Polygonum aviculare*; h – *Rumex obtusifolius*; i – *Viola arvensis*; j – *Urtica urens*; k – *Raphanus raphanistrum*; l – *Capsella bursa-pastoris*; m – *Sinapsis arvensis*; n – *Thlaspi arvense*; o – *Sisymbrium officianale*; p – *Lamium purpureum*; q – *Veronica persica*; r – *Aethusa cynapium*; s – *Senecio vulgaris*; t – *Cirsium arvense*; u – *Sonchus oleraceus*; v – *Tripleurospermum inodorum*; w – *Elytrigia repens*; x – *Poa annu.* An asterisk against a species code indicates that the species did not appear on any plots in that year.

Figure 3a

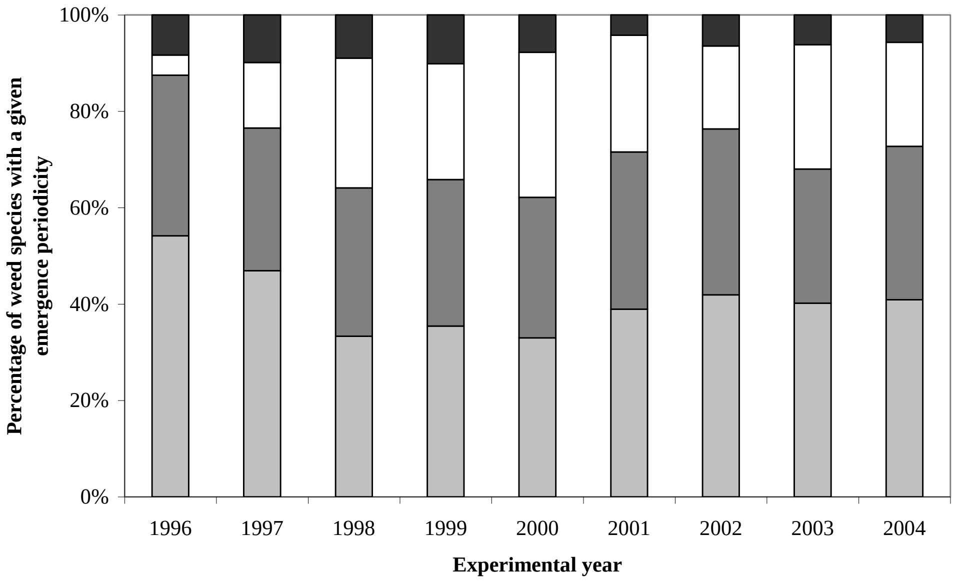

Figure 3b

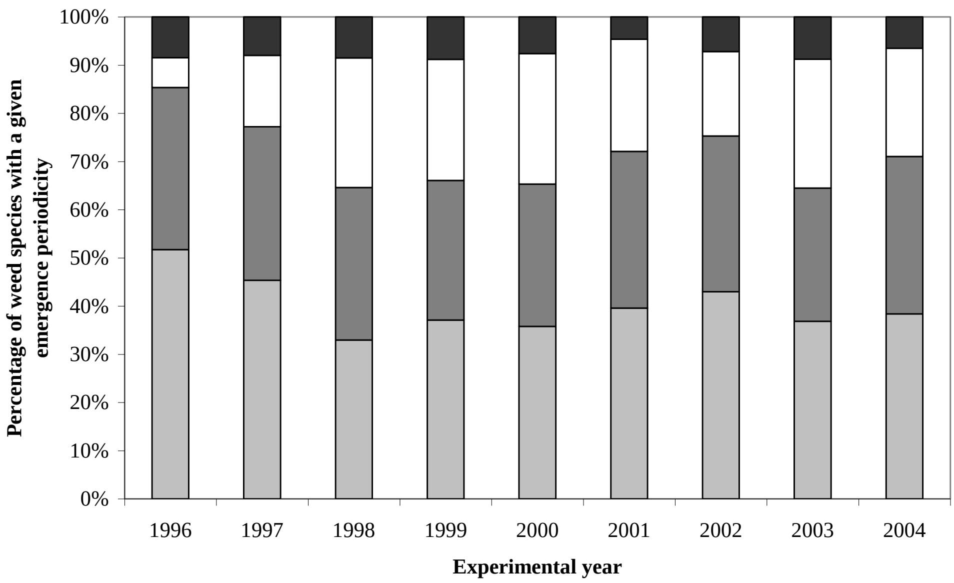

Fig. 3 Relative contributions to the weed flora of species with different emergence periodicities, as defined in Supplementary Table S1, for a) untreated and b) herbicide treated plots in the nine years of the study, where: black = autumn-spring; white = spring only; dark grey = spring-autumn; light gray = generalist.

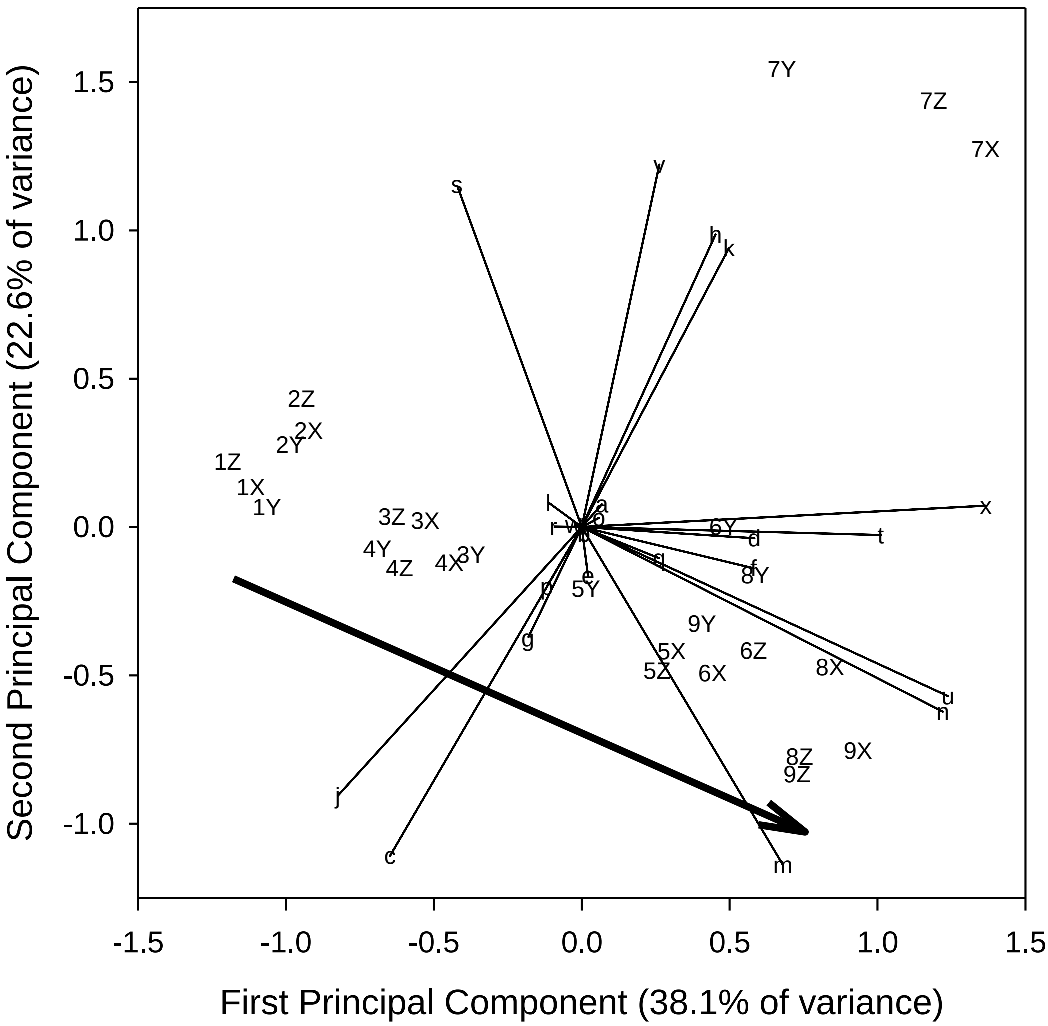

Fig. 4 Biplot displaying the associations between weed species and combinations of year and herbicide application timing, as given by the first two dimensions from a Principal Component Analysis of the weed species presence/absence data averaged across replicates, herbicide products and application rates. Lower-case letters and associated vectors from the origin indicate the weed species loadings (codes as given in Figure 2 – key species are: c – *S. media*, d – *C. album*, f – *P. lapathifolium*, g – *P. aviculare*, h – *R. obtusifolius*, j – *U. urens*, k – *R. raphanistrum*, m – *S. arvensis*, n – *T. arvense*, s – *S. vulgaris*, t – *C. arvense*, u – *S. oleraceus*, v – *T. inodorum*). Numbers and upper-case letters indicate the scores for combinations of year (1 = 1996, 2 = 1997, 3 = 1998, 4 = 1999, 5 = 2000, 6 = 2001, 7 = 2002, 8 = 2003, 9 = 2004) and herbicide application timing (X = pre-emergence, Y = post-emergence, Z = untreated control). Arrow indicates the general trend from the first year to the last year of the study.

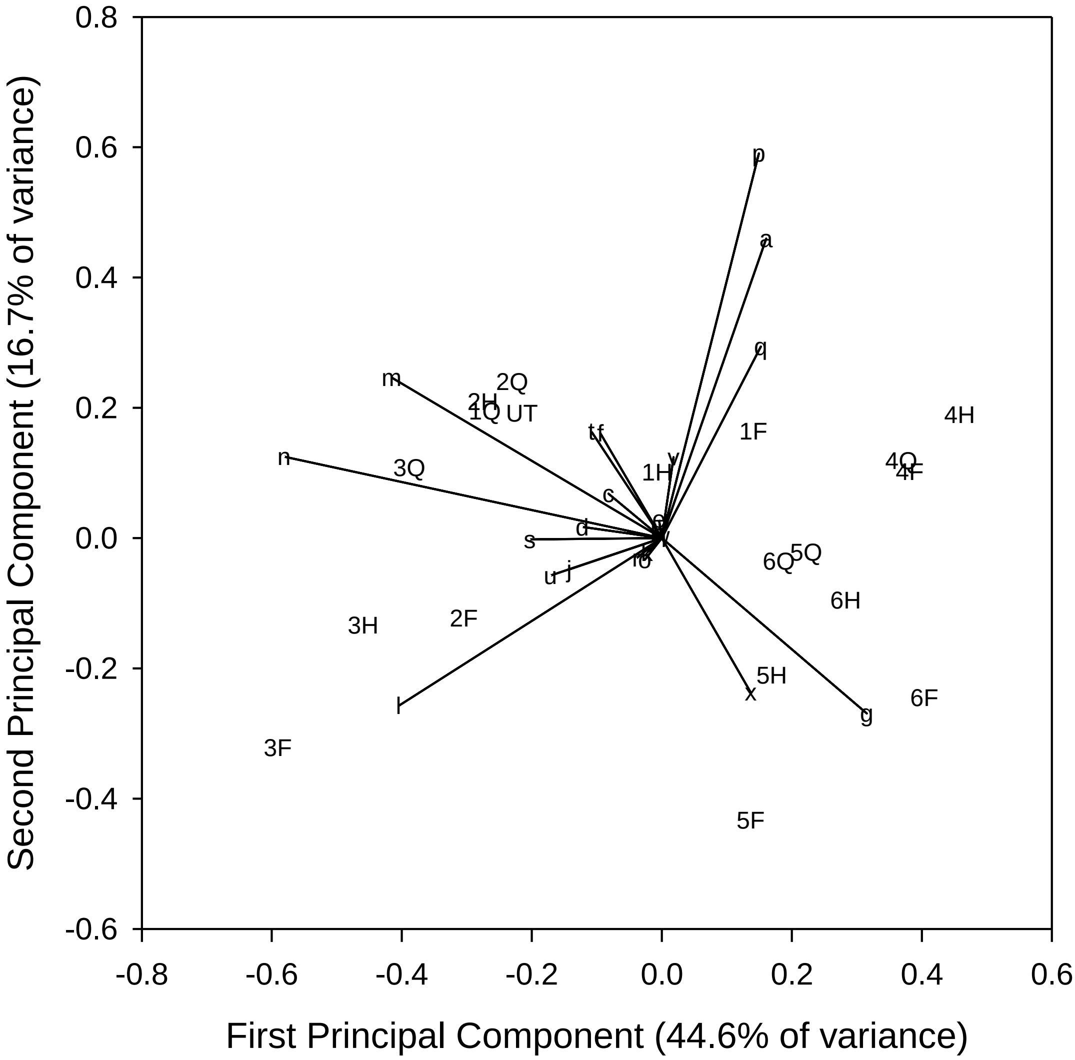

Fig. 5 Biplot displaying the associations between weed species and combinations of herbicide product and application rate, as given by the first two dimensions from a Principal Component Analysis of the weed species presence/absence data averaged across years. Lower-case letters and associated vectors from the origin indicate the weed species loadings (codes as given in Figure 2 – key species are: a – *F. officinalis*, f – *P. lapathifolium*, g – *P. aviculare*, l – *C. bursa-pastoris*, m – *S. arvensis*, n – *T. arvense*, p – *L. purpureum*, q – *V. persica*, s – *S. vulgaris*, t – *C. arvense*, u – *S. oleraceus*, x – *P. annua*). Numbers and upper-case letters indicate the scores for combinations of herbicide product (1 = pre-emergence linuron, 2 = pre-emergence propachlor, 3 = pre-emergence pendimethalin, 4 = post-emergence linuron, 5 = post-emergence ioxynil, 6 = post-emergence bentazone) and herbicide application rate (F = full recommended rate, H = half rate, Q = quarter rate).